

REVIEW

Evolution of the Development and Larval Types in Asteroids

CHITARU OGURO

*Department of Biology, Faculty of Science, Toyama University,
Toyama 930, Japan*



I. INTRODUCTION

What form is the most primitive type of sea-stars and what group is the most advanced has been a long-lasting dispute which remains unsettled. More than half century ago, vehement discussions were held among Bather [1-3], Gemmill [4], MacBride [5-7] and Mortensen [8, 9] on the ancestral type of sea-stars and whether the brachiolaria is a primitive type of sea-star larva or not. Discussion was held on Nature as a stage for the battle. In fact, Mortensen [9] stated "to protest against the character of his unprovoked attack on me". Mortensen took the position that the brachiolaria is a secondarily specialized larval type. Therefore, he is of the opinion that the sucker of the brachiolaria is not a vestigial organ of a fixed stage of ancestral echinoderms. In contrast to the view of Mortensen, Gemmill [4] and MacBride [5-7] convinced that the sucker of the brachiolaria is a typical ancestral feature, and therefore the brachiolaria is a primitive type of sea-star larvae. These contrasting ideas on the phyletic nature of the larval type led to different views on the primitive types of the asteroid species or groups. There is no doubt that Gemmill and MacBride believed that astropectinid and luidid species, in which the larvae bear no sucker, are advanced types of sea-stars. Mortensen believed, as a matter of course, that the species belonging to the Astropectinidae and Luidiidae, are more primitive than species of the other groups

which give rise the brachiolaria with a sucker [9, 10].

Thereafter, not much discussion has been held on the phyletic rank of the Orders of asteroids, although many ideas and revised schemes have been put forth on the relative positions in the higher taxa of asteroids or related groups.

Based on the comparative morphology of existent and extinct species of asteroids and their presumable relatives, Fell [11] proposed a scheme for the possible evolutionary process of asteroids. According to this scheme, Asteroidea and Ophiuroidea rose from a common ancestor, the Somasteroidea, from which he illustrated the transition to modern asteroids through the Platyasterida. Since then, contemporary systematists adopted basically this scheme for asteroid systematics and evolution [12-17].

It is not the primary object of this article to illustrate the evolution of asteroids themselves. Therefore, further discussion on this problem will not take place here. However, it is to be noted that Blake [18] gave a novel idea on the systematics of Asteroidea based on the detailed comparative anatomy in existent and extinct specimens. He noted "No living sea star is primitive in the sense of being close to ancestral sea stars and other echinoderm groups: the Paxillosida, which commonly has been considered primitive, is here considered to be specialized."

Table 1 shows some of the different schemes of the systematic arrangement of Asteroidea (existent groups only are shown).

TABLE 1. Systematic arrangement of sea-stars by selected authors

Fell and Pawson (1966) [12]		Nichols (1969) [14]	
Class Stelleroidea		Class Asteroidea	
Subclass	Somasteroidea	Subclass	Somasteroidea
Subclass	Asteroidea	Subclass	Euasteroidea
Order	Platyasterida	Order	Platyasterida
—	Phanerozonida	—	Phanerozonida
—	Spinulosida	—	Spinulosida
—	Euclasterida	—	Euclasterida
—	Forcipulatida	—	Forcipulatida
Subclass	Ophiuroidea		
Downey (1973) [16]		Blake (1987) [18]	
Class Asteroidea		Class Asterozoa	
Order	Platyasterida	Superorder	Forcipulatacea
—	Paxillosida	Order	Brisingida
—	Valvatida	—	Forcipulatida
—	Spinulosida	Superorder	Valvatacea
—	Forcipulatida	Order	Valvatida
—	Zorocallida	—	Notomyotida
—	Euclasterida	—	Paxillosida
		Superorder	Spinulosacea
		—	Valvatida
		—	Spinulosida

II. DEVELOPMENTAL TYPES

Before going on to discuss the evolution of larval types of asteroids, it would be helpful to give a brief survey for understanding the discussion on the development of asteroids and its classification. Development of the sea-star is classified into four types by what type of larvae appear, as shown in Figure 1 [19, 20].

a. Indirect type of development

In this type of development, the larva passes through two apparently different stages, viz. bipinnaria and brachiolaria (Fig. 1, I-1~I-4). Slightly after the commencement of gastrulation, the tip of the archenteron bulges laterally. These bulges become coelomic pouches. The coelomic pouches are separated from the archenteron and differentiated, each into an anterior coelom and a posterior coelom. The archenteron differentiates into a larval esophagus, stomach and intestine. The

mouth opens at the ventro-anterior portion of the larva and the blastopore becomes the anus.

Along with the internal changes noted above, several projections appear at the anterior and lateral portions of the larval body. These projections are called the bipinnarian arms and the larvae bearing the bipinnarian arms are called bipinnariae (Fig. 1, I-2). Two heavily ciliated bands, preoral and postoral, appear in the anterior and posterior portions, the former being called the preoral ciliary band, and the latter, the postoral ciliary band.

Bipinnariae feed on planktonic algae and grow for a certain period of time. The full grown bipinnaria bears five pairs of bipinnarian arms. Then three new processes are formed on the anterior part of the bipinnaria. They are different from the bipinnarian arms since they contain a part of the coeloms inside. The larvae with brachiolar arms are called brachiolariae (Fig. 1, I-3). In the majority of the brachiolaria, a sucker which was one the foci of the discussion among Bather,

Gemmill, MacBride and Mortensen, as described before, is formed among the brachiolar arms. During the later bipinnarian stage and the brachiolarian stage, organogenesis proceeds inside the larval body for the adult structure. In the late brachiolaria, the adult rudiment is formed on the posterior portion of the larval body. Close to the metamorphic climax, the anterior portion of the larval body begins to degenerate and the brachiolaria sinks to the substratum. The sucker, together with the papillae on the brachiolar arms, functions to fix to the substratum. The eggs of the species of the indirect type are poor yolky and small (120–250 μm in diameter).

Thus, the indirect type of development is characterized by two larval types, feeding bipinnaria and feeding brachiolaria. The following are some of the species having this type of development: *Culcita novaeguineae* [21], *Archaster typicus* [10], *Lincxia laevigata* [21], *Porania pulvillus* [22], *Stichaster australis* [23], *Acanthaster planci* [24], *Acanthaster brevispinus* [25], *Asterina pectinifera* [26, 27], *Coscinasterias calamaria* [23], *Asterias rubens* [28].

The term "development with bipinnaria and brachiolaria" is suggested instead of the indirect type of development to show more clearly the larval types to pass [29, 30]

b. Direct type of development

In this type of development, the larva passes through only 1 stage, the brachiolaria (Fig. 1, D-1~D-3). However, the shape of the brachiolaria of this developmental type is quite different from that of the indirect type.

After passing through the gastrula stage, the blastopore closes. The external form does not change for a certain period of time. Then it takes a bilobed form. This larva possesses no functional digestive system and is lecithotrophic. However, internal organogenesis proceeds as in the bipinnaria of the indirect type. One projection emerges from the anterior portion and two projections from the ventro-anterior portions of the larva. As a result, the larva takes a sort of snow-man shape (Fig. 1, D-2). These three projections are the brachiolar arms since they are lined with embryonic coelom, although they are different in form from the brachiolaria in the indirect develop-

ment. A sucker (fixing disk) appears among the brachiolar arms. Tips of the brachiolar arms and the sucker bear an adhesive apparatus and are utilized for fixing to the substratum as in the brachiolaria of the indirect type.

It is noteworthy that the eggs of the species having the direct type are rich in yolk and large ($>400 \mu\text{m}$). The larval mouth and anus are not formed and the brachiolaria of the direct type is a non-feeding larva, as noted before. After a certain period of time as a free-swimming larva, the adult rudiment appears in the posterior portion. During the metamorphic climax, the anterior portion is absorbed into the posterior portion, the adult rudiment.

The species noted below are some of the representatives having the direct type of development.

Mediaster aequalis [31], *Certanardoa semiregularis* [32], *Henricia sanguinolenta* [33], *Crossaster papposus* [34], *Solaster endeca* [35], *Asterina gibbosa* [36], *Asterina coronata* [37], *Asterina minor* [38], *Pteraster tessellatus* [39], *Leptasterias hexactis* [40].

The term "development with brachiolaria" is suggested instead of the direct type of development [29, 30].

c. Nonbrachiolarian type of development

In contrast to the case of the direct type of development, which lacks the bipinnaria stage, the nonbrachiolarian type of development does not pass through the brachiolarian stage during larval development (Fig. 1, NB-1~NB-3). In this developmental type, metamorphosis takes place while the bipinnaria is still planktonic. Internal organogenesis proceeds for the adult structure in the metamorphosing bipinnaria as in the brachiolaria in the indirect and direct types. However, metamorphosing larvae do not bear brachiolar arms and suckers which would appear in the brachiolaria, utilized for the settlement of metamorphosing brachiolaria to the substratum.

The following species are known to occur with this type of development. *Luidia ciliaris* [41], *Luidia sarsi* [42], *Luidia quinaria* [43], *Astropecten irregularis* [44], *Astropecten aranciaceus* [45], *Astropecten scoparius* [19]. Eggs of these species are poor yolky and small ($<250 \mu\text{m}$).

BIPINNARIA BRACHIOLARIA

INDIRECT

I-1



I-2



I-3

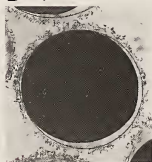


I-4



NONBRACHIOLARIAN DIRECT

D-1



D-2



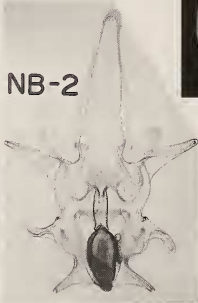
D-3



NB-1



NB-2



NB-3



WITH BARREL-SHAPED LARVA

BARREL-SHAPED LARVA

B-1



B-2



B-3



It is of interest that all species having the non-brachiolarian type of development belong to the family Luidiidae and Astropectinidae. No species belonging to groups other than Luidiidae and Astropectinidae are known to have the non-brachiolarian type of development. The fact that the nonbrachiolarian type occurs in very limited systematic groups shows that at least some of the developmental types are intimately related to the systematic position in sea-stars. This might give a logical base for discussing the evolution of the larval type of sea-stars.

The term "development with bipinnaria only" is suggested instead of the nonbrachiolarian type of development to show more clearly the larval type to pass [29, 30].

d. Development with barrel-shaped larva

Two types of sea-star larvae, bipinnaria and brachiolaria, the latter having two forms, had been known until the barrel-shaped larva was discovered in *Astropecten latespinosus* by Komatsu [46]. In this species, the embryos reach the gastrula stage after passing through the wrinkled blastula and then the blastopore closes. Neither the larval mouth nor anus opens. Until the commencement of metamorphosis, the larvae retain their barrel-shape or ovoid shape without emerging brachiolar arms and suckers (Fig. 1, B-2). Therefore, the term, barrel-shaped larva, was given to this type of sea-star larva.

The barrel-shaped larvae are planktonic and swim with the cilia which uniformly cover the entire surface of the larval body. However, the internal organogenesis of the adult organs proceeds as in the brachiolaria of the direct type. The adult rudiment appears on the posterior portion of the barrel-shaped larva when metamorphosis begins. Metamorphosing larvae sink to the substratum as the anterior portion of the larva begins to degenerate and be absorbed into the posterior

portion. Details of the morphology of the barrel-shaped larva of *Astropecten latespinosus* has been recently described [20].

This type of development has so far been observed in only three species, *Astropecten latespinosus* [46], *Astropecten gisselbrechti* [48] and *Ctenopleura fisheri* [49]. It is of considerable interest that all three species belong to the family Astropectinidae. This gives another cue to discuss the evolution of sea-star larva as will be described later.

III. RELATION BETWEEN DEVELOPMENTAL TYPE AND SYSTEMATIC POSITION

Development of the sea-stars has been reported in more than one hundred species, including fragmentary observations. However, details of development from fertilization through metamorphosis have been known in only about thirty species. Although nothing has been known on the development of species belonging to Zorocallida and Eulasterida, knowledge on the development of some representatives in the other five orders (according to Downey's system) is available to some extent.

Table 2 shows the relationship between developmental types and systematic groups. As is apparent from this table, the indirect and direct types of development occur in four Orders (Paxillosida, Valvatida, Spinulosida, and Forcipulatida). Therefore, these two types have no intimate relation to the systematic position of sea-stars.

This is well exemplified in the development of species belonging to the subfamily Asterininae, whose development has been fairly well documented. The direct development has been reported in *Asterina gibbosa* [36], *Patiriella exigua* [8], *Asterina coronata japonica* [37], *Patiriella vivipara* [50], *Asterina batheri* [47], *Asterina minor* [38]. Two asterinid species, *Patiria minata* [51] and

Fig. 1. Four developmental types of asteroids and their typical larvae shown by photographs of stages to pass through. I-1~I-4, Indirect type: I-1, Fertilized ova; I-2, Bipinnaria; I-3, Brachiolaria; I-4, Newly metamorphosed juvenile. D-1~D-3, Direct type: D-1, Fertilized ova; D-2, Brachiolaria; D-3, Newly metamorphosed juvenile. NB-1~NB-3, Nonbrachiolarian type: NB-1, Fertilized ova; NB-2, Bipinnaria; NB-3, Newly metamorphosed juvenile. B-1~B-3, Development with barrel-shaped larva: B-1, Fertilized ova; B-2, Barrel-shaped larva; B-3, Newly metamorphosed juvenile.

TABLE 2. Relationship between developmental type and systematic group (after Downey [16])

Developmental type	Larval type	Order	Remarks
Indirect	Bipinnaria & brachiolaria	Paxillosida Valvatida Spinulosida Forcipulatida	except Astropectinidae
Direct	Brachiolaria	Paxillosida Valvatida Spinulosida Forcipulatida	except Astropectinidae
Nonbrachiolarian	Bipinnaria	Platyasterida Paxillosida	Astropectinidae only
With barrel-shaped larva	Barrel-shaped larva	Paxillosida	Astropectinidae only

TABLE 3. Relation between egg size and developmental type in asterinid species

Species	Egg diameter (μm)	Developmental type
<i>Asterina pectinifera</i>	170	Indirect
<i>Patiria miniata</i>	185	Indirect
<i>Asterina coronata japonica</i>	420	Direct
<i>A. batheri</i>	430	Direct
<i>A. minor</i>	435	Direct
<i>A. burtoni</i>	450-500	Direct
<i>A. gibbosa</i>	500	Direct
<i>A. pseudoxigua pacifica</i>	700	Direct

Asterina pectinifera [27], undergo the indirect development. Thus, these two types of development occur in species belonging to a subfamily and even to a genus (*Asterina*).

Questions arise on aspects of two separate ways of development, direct or indirect, in the asterinid species. Size or quantity of yolk content in the egg has been suggested as a primary factor to determine the type of development in echinoderms [40, 52]. Development of the asterinid species seems not to be precluded from this general rule, as shown in Table 3.

It is obvious from this table that eggs less than 200 μm in diameter take the indirect type and those larger than 400 μm in diameter develop through the direct type. It is clear that taking either the indirect or the direct type depends upon the size of the egg. Systematic position contributes

nothing to this dichotomous choice.

In contrast to the situation in the indirect and direct types, the nonbrachiolarian type of development occurs in a very limited group of sea-stars (viz. in 2 families, Astropectinidae and Luidiidae). As well, development with the barrel-shaped larva has been reported only in Astropectinidae. It is therefore reasonable to conclude that these 2 developmental types are linked to the systematic position of the species.

IV. EVOLUTION OF THE DEVELOPMENT AND LARVAL TYPES

The term "dipleurula" was first proposed for a hypothetical common ancestor of Echinoderm. It is bilaterally symmetrical organism with a simple digestive tract and a pair of hydrocoel, each having

a hydropore. The whole body is covered by cilia or a single loop ciliary band which encircles the body. As is assumed from the bilateral organization, the "dipleurula" was put as having a bottom creeping nature. However, no one today believes such an organism is an ancestor of existent echinoderms. Instead, "dipleurula" is now given as a type of basic echinoderm larva from which most of the various later larvae are derived.

It has been well accepted that basic types of marine invertebrates produce a large number of poor yolky eggs and emerged larvae are feeding and pelagic [53]. In fact, poor yolky eggs of small size are most commonly observed in marine invertebrates. On the other hand, marine invertebrates adapted to deep sea or high latitude produce a small number of yolky and large eggs [52]. This is understood to be the most economical and efficient way in reproductive strategy, with a limited total energy in a severe environment.

If reproductive strategy of echinoderms, including asteroids, takes place along this general line, the most basic type of echinoderm eggs should be poor yolky and of small size. As well, larvae emerged from such eggs are feeding and pelagic. The basic pattern of this larva should follow the basic design of the dipleurula, even the dipleurula is purely imaginary.

According to this concept, the indirect or the nonbrachiolarian development must be of the basic pattern in sea-star development. As a consequence, the direct type of development is denoted as differentiated or advanced as shown in Figure 2.

As described before, the indirect and direct types are commonly found and not linked to the systematic position of species. Thus, it is understandable that A→B transition could have occurred. Actually, the final larval form before the initiation of metamorphosis in either type is the brachiolaria, which bear a sucker and adhesive

papillae on the brachiolar arms.

In the indirect type, poor yolky eggs give rise to planktonrophic bipinnariae, which feed on planktonic algae and grow into a different type of larvae, brachiolariae which furnish with structures necessary to complete metamorphosis. On the other hand, larvae emerged from yolky eggs grow without feeding, but use the deposited yolk material for energy and constructive sources [54, 55]. Thus, the bipinnaria stage in the indirect type is a necessary stage to nurse the larvae to grow to a certain stage in which they are prepared enough for taking on metamorphosis. In large and yolky eggs, this trophogenic and growing stage has been omitted. In fact, some authors have called the direct development a shortened or abbreviated development [8, 56]. This is of course based on the concept that the original type of sea-star development passes through the two-step larval stage, but the later trophogenic stage retrogressed as they become acquired yolk material. Strathmann also suggested that the ancestral echinoderm had feeding larva [57].

The next question is which type is more primitive or basic in sea-star development, the indirect or the nonbrachiolarian type. If one takes a position for accepting that the dipleurula type larva is more basic, although no known echinoderm has only a dipleurula type as pointed out by Nichols [14], the conclusion is narrowed to the idea that the nonbrachiolarian type is the more basic. In the nonbrachiolarian type of development, the larva is of only one type, which is of dipleurula type, while the indirect type bears two types of larvae. This conclusion is fortified by the following:

(1) As noted earlier, Paxillosida and Platysteirida have been generally considered as primitive groups among existent asteroids. The fact that the nonbrachiolarian development occurs only in Astropectinidae (Paxillosida) and Luidiidae

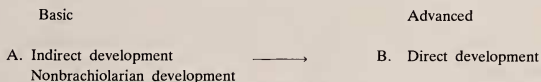


Fig. 2. A possible transition of the developmental type in association with the change from poor yolky eggs to yolky eggs.

(Platyasterida) may indicate that this developmental type is the most primitive, which has been persistently conserved in these primitive groups of sea-stars.

(2) The brachiolar larvae of both the direct type and indirect type species take a specialized form preparing for metamorphosis by having a central sucker and adhesive papillae on the brachiolar arms, although different in contour. It can thus be recognized that brachiolaria is a larval form which is designed to accomplish metamorphosis by settling on the substratum, furnished with a specialized fixing apparatus.

One may intend to believe that the bipinnaria of the nonbrachiolarian type is a larval form with degenerated fixing apparatuses by an adaptation to a mud or fine sand bottom [7]. However, it does not seem to be correct. In *Astropecten scoparius* and *Luidia quinaria*, the larvae in the late stages of metamorphosis and juveniles just after the completion of metamorphosis are furnished with suckered tube-feet, although the adult tube-feet are suckerless. They utilize these tube-feet to fix to the substratum [19, 43]. Thus, the fixing apparatus is so necessary for the metamorphosing larvae of these astropectinid and luidid species, as well as in all species of the other sea-star groups. Therefore, it is hardly acceptable that the fixing apparatus has degenerated by adaptation of the metamorphosing larvae to a mud or sand bottom. In contrast, suckerless tube-feet of the adult may be attributable to a result of the adaptation of the adult to mud or sand substrata.

This means, for one thing, that the fixing apparatus of the metamorphosing larvae is of a later

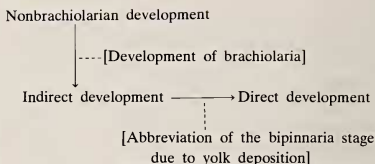


FIG. 3. Evolution of developmental type and factors or phenomena involved.

character, acquired in advanced groups of sea-stars, to ensure efficient progress of metamorphosis. Thus, the step is shown in Figure 3.

Discussion has so far been concerned to three types of development and two types of larvae (bipinnaria and brachiolaria). However, further questions should be presented on the status of the barrel-shaped larva and development with the barrel-shaped larva.

As described before, this type of larva has been found only in species belonging to the family Astropectinidae. Furthermore, all other species of Astropectinidae described so far develop through the nonbrachiolarian type. These facts suggest an intimate affinity between the nonbrachiolarian development and the development with the barrel-shaped larva. In fact, it was pointed out that early formation of the madreporic plate and precocious tube-feet formation in the metamorphosing larvae are characteristic features occurring only in these 2 developmental types [19, 20, 43, 46, 48, 49].

These facts all indicate that the development of barrel-shaped larva is a modification of the nonbrachiolarian type of development as suggested by

TABLE 4. Relation between the egg size and developmental types in astropectinid species

Species	Egg diameter (μm)	Developmental type
<i>Astropecten polyacanthus</i>	160	Nonbrachiolarian
<i>A. aranciatus</i>	200	Nonbrachiolarian
<i>A. irregularis</i>	210	Nonbrachiolarian
<i>A. scoparius</i>	230	Nonbrachiolarian
<i>A. latespinosus</i>	300	With barrel-shaped larva
<i>A. gisselbrechti</i>	350	With barrel-shaped larva
<i>Ctenopleura fisheri</i>	460	With barrel-shaped larva

Komatsu and Nojima [48]. Furthermore, it is extended to the idea that the barrel-shaped larva is a modified bipinnaria of the nonbrachiolarian type.

It is of special interest that the size (yolk content) seems here again to be the most decisive factor for having either type of larva in astropectinid species as shown in Table 4.

A conclusion is drawn from this table that eggs larger than 300 μm in diameter develop through the barrel-shaped larva and smaller than that through the bipinnaria of the nonbrachiolarian type. As suggested before, it is now reasonable to conclude that the barrel-shaped larva is a modified bipinnaria of the nonbrachiolarian type, brought about by yolk deposition. This leads to the scheme shown in Figure 4.

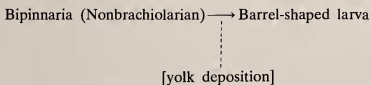


FIG. 4. Transition of the larval type in association with yolk deposition in astropectinid species.

Affinity between the barrel-shaped larva and the brachiolaria of the direct type may be of special interest, since they resemble each other in external form.

It seems that acquisition of the oval shape is a basic feature in larvae emerged from yolky eggs in echinoderms, since this can be seen in species in other Classes, too. Here only few representatives are listed in Table 5.

As described before, transition from the indirect type to the direct type, due to the yolk deposition,

brought about an oval or snow man-shaped, brachiolaria. If the same could happen in the nonbrachiolarian type, yolk deposition would cause transition from the bipinnaria to an oval shaped larva. However, in primitive sea-stars, which develop through nonbrachiolarian development, an ability to develop brachiolar arms and fixing apparatus has not yet been evolved. The resultant larva is presumed to be an oval without brachiolar arms and sucker. Of course, this is nothing but the barrel-shaped larva.

This idea is in perfectly conformity with the facts shown in Table 4, indicating that smaller eggs pass through the nonbrachiolarian development while larger eggs emerge the barrel-shaped larva.

Therefore, the barrel-shaped larva and the brachiolaria of the direct type should be placed in very distant positions, although they resemble each other in a sense. Figure 5 shows the integrated construction of a possible evolutionary process of larval types together with developmental types.

The following is a summary of the discussion described above. The most primitive type of development is the nonbrachiolarian development which can now be observed only in luidiid (Platyasterida) and astropectinid (Paxillosida) species (Fig. 5, 2~4). The only larva appearing in this developmental type is the bipinnaria. As a result of yolk accumulation in some species of this group by adaptive promotion to certain environmental conditions, the bipinnaria is transformed into the barrel-shaped larva, which is a fundamental form of yolky and non-feeding echinoderm larva (Fig. 5, 5~7). This is one line of changes in larval form and developmental types occurring in a limited primitive groups. A common feature found in

TABLE 5. Some representatives of oval shaped larvae with rich yolk in 3 other echinoderm Classes

Ophiuroidea	<i>Ophiolepis cincta</i> Mortensen, 1921 [8]
	<i>Amphioplus abditus</i> Hendler, 1977 [58]
Echinoidea	<i>Heliocidaris erythrogramma</i> Mortensen, 1921 [8]
	<i>Asthenosoma ijimai</i> Amemiya & Tsuchiya, 1979 [59]
Holothuroidea	<i>Cucumaria echinata</i> Ohshima, 1921 [60]
	<i>Scoliodotella uchidai</i> Oguro, 1971 [61]

these larvae is lacking in the specialized fixing apparatus that can appear in more advanced groups. They utilize their tube-feet, which are precociously formed in metamorphosing larvae, for fixing to the substratum during metamorphosis.

Additionally, more advanced sea-star groups come to have more advanced type of larva furnished with fixing apparatuses for settlement to the substratum at metamorphosis. This advanced larval type is called the brachiolaria. As a result, these species come to have a two-step larval stage,

one for growing and the other preparing for metamorphosis (Fig. 5, 8~11).

However, if yolk deposition occurs by taking an advantage in reproductive strategy, abbreviation of the growing stages occurs. The resulting larvae are inevitably oval (Fig. 5, 12~14). They are different from the barrel-shaped larva by being furnished with a specialized fixing apparatus. Thus, brachiolaria of the direct type should be the most specialized type among sea-star larvae. The contents are illustrated in Figure 5.

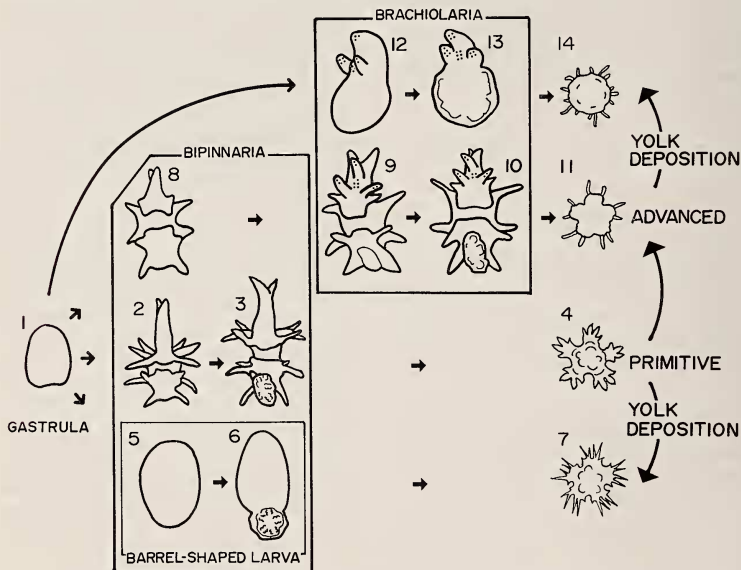


FIG. 5. A scheme showing the possible process of evolution of the larval type and developmental type. From left to right, the actual developmental process.

1~4. Primitive or basic process of development (nonbrachiolarian development), occurring only in species belonging to Luidiidae and Astropectinidae.

1, 5~7. Development (development with barrel-shaped larva) derived from [1~4] (nonbrachiolarian development) by yolk deposition in the egg, occurring only in species belonging to Astropectinidae.

1, 8~11. Advanced developmental process (indirect development) with the evolution of specialized type of larva (brachiolaria), which is furnished with fixing apparatuses. Dotted areas show the presence of fixing apparatus.

1, 12~14. Development (direct development) derived from [1, 8~11]. Abbreviation of the growing stage (bipinnaria) is consequent on the yolk deposition in the egg. Dotted areas show the presence of the fixing apparatus.

ACKNOWLEDGMENTS

The author wishes to express his cordial thanks to Dr. Miéko Komatsu for her helpful discussion and for providing photographs used in this article.

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